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FRUCTIFICATION OF ARMILLARIA MUCIDA

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On the Development of the Fructification of Armillaria mucida, Schrad.

BY

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With Plate XXXV.

ARMILLARIA MUCIDA is a hymenomycetous fungus commonly met with in England wherever the beech grows. Its fruit-bodies appear in autumn, growing in tufts on the diseased portions of beech trees, and are readily identified by the (usually) intense white of the pileus, which, further, is covered with a mucilaginous coating.

The fungus is fairly abundant on the older beech trees in Windsor Park, where it seems to be doing considerable harm.

There appears to be some diversity of opinion as to its true parasitic nature, and partly for this reason I undertook a study of its life-history, the results of which will be embodied in a separate paper. The opportunity for tracing the course of the development of the fructification naturally presented itself, and this forms the subject of the present note.

Comparatively little attention has been given to the development of the fructification in Hymenomycetes. One of the most recent papers on the subject is that of G. F. Atkinson on *Agaricus campestris* (1), in 1906. Prior to this paper no detailed study of the development appears to have been made since Fayod's work (3) in 1889.

Atkinson gives an historical sketch of previous work in this direction in the paper quoted above; consequently no lengthy *résumé* need be given here.

Atkinson suggests, apparently with justification, that the earlier investigators did not examine sufficiently young specimens, and they seem to have been led to general conclusions which do not hold good at any rate in all cases.

De Bary in the case of *Agaricus campestris* (2) and R. Hartig in that of *Armillaria* (*Agaricus*) *mellea* (5) describe the veil (*velum partiale* of Fries) as developing by new growth. They find that at an early stage a circular

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channel, in the form of a narrow ring open towards the outside, arises in the upper part of the body by means of separation of the tissues. The portion above becomes the pileus and that below the stipe. By later growth, downwards from the pileus and upwards from the stipe, two interweaving series of hyphae are formed, thus giving rise to the veil, which covers the air-space. Atkinson observed a very different course of development in *Agaricus campestris*. He supposes that De Bary may not have studied the very young stages, and states that it would seem that 'he adopted Hartig's suggestion that *Agaricus campestris* followed the same course as that described by Hartig for *Agaricus melleus*', and in this way the statements current in textbooks (4) may have originated.

Having obtained a number of young fructifications of *Armillaria mucida* in pure cultures, I undertook a study of the development of the veil in that species, and, as will be seen, my observations agree essentially with those of Atkinson.

Atkinson seems to accept Hartig's account of the development in *Armillaria mellea* as substantially correct, but believes that De Bary was mistaken in admitting a similar process for the case of *Agaricus campestris*. As a result of my own investigation I am led to the conclusion that either Hartig's observations must be faulty, for the reason put forward by Atkinson, or else the development in two such closely allied species as *Armillaria mellea* and *A. mucida* is entirely divergent. I venture to suggest that such a divergence is not probable, and that the course of development is similar to that described by Atkinson for *Agaricus campestris* and as set forth below for *Armillaria mucida*. It must also be remembered that at the date of Hartig's work the improved methods we can now command were unknown.

The fungus was grown on bread and on sterilized beech wood, and sporocarps in all stages were taken for the investigation. Three naturally-grown very young carpophores were also obtained for comparison; no differences were found between those from the two sources.

At first I failed to realize at what a very early period differentiation of the tissues took place, and had to take specimens of a much younger age. Before there is any external indication of a distinct separation of the pileus, there is an internal differentiation of the tissues, as described later.

The sporocarps were fixed in chromo-acetic acid and microtomed. The sections were stained with various stains. Eosin gave very good results, though, unfortunately, the stain is not lasting. Gentian violet followed by orange G or Bismarck brown was also used, as well as Heidenhain's alum-haematoxylin followed by orange G. The latter method gave the most satisfactory results. All the drawings were done with the aid of the *camera lucida*.

The youngest stages examined, about half a millimetre in length,

presented a homogeneous tissue ; the hyphae ran longitudinally, interweaving freely. Soon, the tissue at the apex becomes looser in texture, leaving, however, an unaltered layer round the periphery (Pl. XXXV, Fig. 1). The hyphae near the apex, which hitherto all ran in the same direction, now begin to display a tendency to radiate towards the periphery, and rapidly form a subcuticular layer of hyphae at right angles to the outer surface (Fig. 2). These hyphae, which are somewhat closely packed to form a sort of palisade tissue, are not differentiated, but are rich in protoplasm, and take a deeper stain. The universal veil can be clearly distinguished now as a layer of hyphae, two or three deep, traversing the ends of the hyphae composing the palisade tissue (Figs. 3 and 4). The veil generally takes a brown stain with haematoxylin and orange G, contrasting well with the violet tint of the adjacent cells.

Hartig considered that *Armillaria mellea* was devoid of a universal veil, but Fayod (3) has shown that such a tissue always exists, though it is sometimes so tenuous as to escape attention.

We have seen that the differentiation of tissues begins at a very early stage and marks off the stipe from the pileus, the latter being defined by the palisade layer. This layer rapidly becomes more confirmed and spreads inwards from its outer and lowermost edge, at the same time assuming a marked palisade character. By this time, too, the pileus is externally distinguishable as a minute cap. The radial palisade layer spreading inwards forms the *primordium of the hymenium.*

Strong surface-growth now causes the pileus to assume greater convexity, at the same time, owing to cessation of growth of the tissues immediately below, the primordium of the hymenium becomes separated from them and a small air-space is formed, which is the origin of the 'gill cavity'. Meanwhile, the outline of the future stipe has become more clearly defined by the outer layers growing looser in texture, so that a mass of lacunae filled with air arises, whereas the future stipe remains densely felted. This, no doubt, assists in supplying the necessary air for the formation of the gill cavity, as pointed out by Atkinson (Fig. 5).

Up to this stage the universal veil has kept pace with the growth of the inner tissues, now, however, its hyphae begin to disintegrate and break up, not only over the surface of the pileus, but also down the sides of the stipe (Fig. 6 ~~and 7~~).

It may be noted here that at this time the decomposing universal veil is very delicate and apt to be torn off even by the microtome blade, so that in some of the sections no veil can be seen. Further, the pileus has taken a more rounded form and is growing in diameter more rapidly than the stipe, so that it bulges somewhat beyond the latter. The disappearance of the veil accentuates this overlapping (Fig. 6). It would seem possible that these phenomena combined to mislead Hartig.

The pileus assumes a globular shape by continued growth, still further separating the hymenium from the 'neutral tissue', which increases the depth of the gill cavity (Fig. 7).

The size of the sporophores does not necessarily correspond with the degree of development, so that it is not possible to indicate the stages of growth by external description. ~~This will be seen by comparing Figs. 5 and 6, both drawn to the same scale, 5 being the younger stage.~~

Soon after the last described stage the lower portion of the pileus begins to grow out and upwards, stretching the neutral tissue to which it is still attached by its margin (Fig. 8).

By this time the universal veil has entirely disappeared, as also the loose lacunar tissue which surrounded the stipe and was previously covered by the veil. It is at this stage that the mucilaginous coating begins to appear on the surface of the pileus.

The neutral tissue is much drawn out by the outward growth of the pileus, and becomes very loose and almost diaphanous by the separation of its elements. This is the *velum partiale*. Sooner or later it is ruptured at the edge of the pileus, sometimes not till the latter is nearly horizontal, remaining attached to the stipe as the *annulus superus*.

During this last period of development the hymenial layer differentiates its elements of basidia, paraphyses, and cystidia. The spores are formed before the rupture of the veil, and I found them capable of germination even when the veil had to be pierced to obtain them.

The mucilage of the pileus is derived from the disintegration of the extremity of the palisade layer laid bare by the disappearance of the universal veil, the remainder of the palisade layer persisting. That the mucilage is due to decomposition and is not merely a secretion is evidenced by the particles and rounded cells found embedded in it (Fig. 8). The mucilage gave an acid reaction with litmus paper.

Summarized, the results are as follows:—

I. A universal veil exists which disintegrates after the differentiation into primordial stipe, pileus, and hymenium.

II. The origin of the hymenium is *endogenous*.

III. There is no separation of pileus and stipe by the formation of an annular air-space.

IV. The marginal veil (*velum partiale*) *is not an aftergrowth*, but is formed by the neutral tissue, which is present from the beginning.

V. The mucilaginous coating of the pileus is derived from the degeneration of the apical portion of the palisade tissue.

An early examination of the very young stages of the sporophores of *Armillaria mellea* seems called for. This species is readily cultivated in the laboratory (see Brefeld's 'Untersuchungen aus dem Gesamtgebiet

der Mykologie'), so that a sufficient supply of carpophores in all stages of development could be secured without difficulty.

I embrace this opportunity to express my best thanks to Professor J. B. Farmer, F.R.S., at whose suggestion this study was undertaken, for his kind encouragement, and to acknowledge my indebtedness to his valuable advice.

Literature quoted.

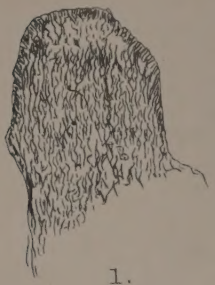
1. Atkinson, G. F.: Development of *Agaricus campestris*. Botanical Gazette, vol. xlii, 1906.
2. De Bary: Morphologie und Physiologie der Pilze. 1886.
3. Fayod: Prodrome d'une histoire naturelle des Agaricinées. Ann. Sci. Nat., Bot., vii, 9, 188.
4. Goebel: Outlines of Classification and Special Morphology of Plants. English edition. 1887.
5. Hartig, R.: Wichtige Krankheiten der Waldbäume, &c. 1874.

Explanation of figures in Plate XXXV.

Illustrating Mr. Fischer's paper on the Development of the Fructification of *Armillaria mucida*, Schrad.

Fig. 1. Young stage showing loose texture in centre of the undifferentiated sporophore. × about 35.
Fig. 2. Subcuticular palisade layer forming the primordium of the pileus. × about 35.
Fig. 3. The same enlarged to show details of structure and the *velum universale*. × about 470.
Fig. 4. Somewhat further accentuated palisade tissue. × about 470.
Fig. 5. Sporophore showing primordium of the hymenium, the gill cavity and the lacunar texture of the subcortical tissue covering the stipe. × about 35.
Fig. 6. Further stage—the universal veil beginning to disintegrate. × about 470.
~~Fig. 7. The same enlarged to show details. × about 470.~~
Fig. 7. The universal veil and loose tissue around the stipe have entirely disappeared. The neutral tissue is still attached to the margin of the pileus. × about 25.
Fig. 8. Section through pileus of ripe carpophore to show decomposition of the outer part of the palisade tissue to form mucilage. × about 315.

Royal College of Science, South Kensington.
May, 1909.



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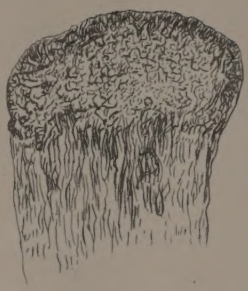

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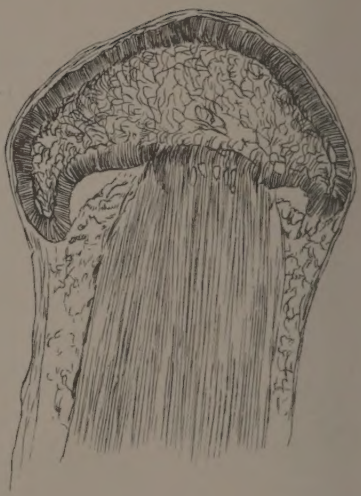

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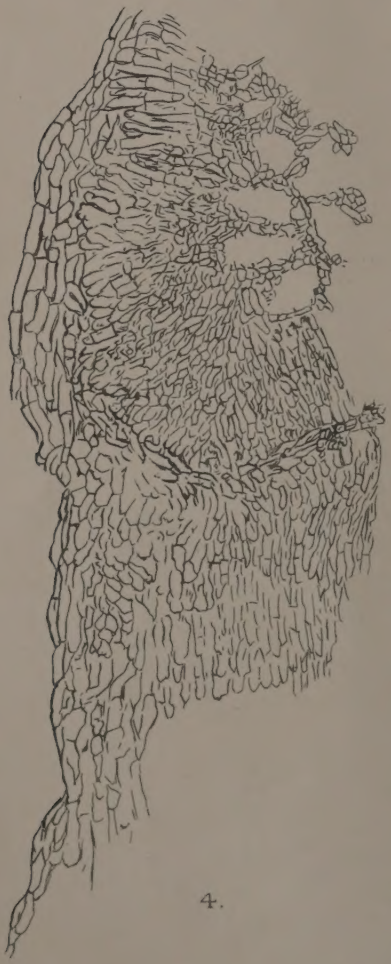

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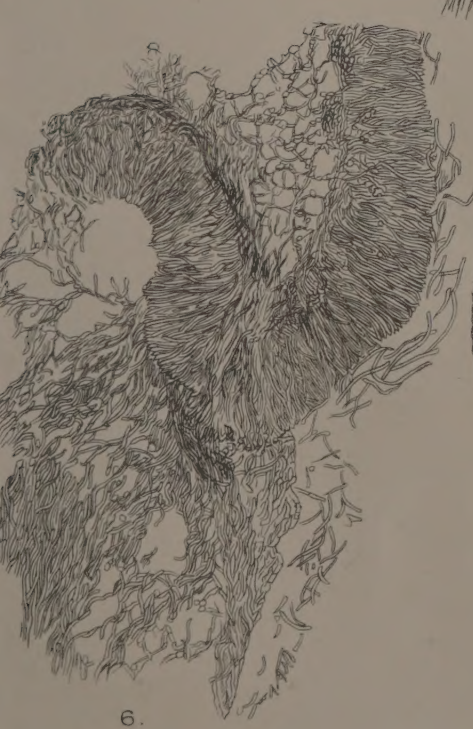

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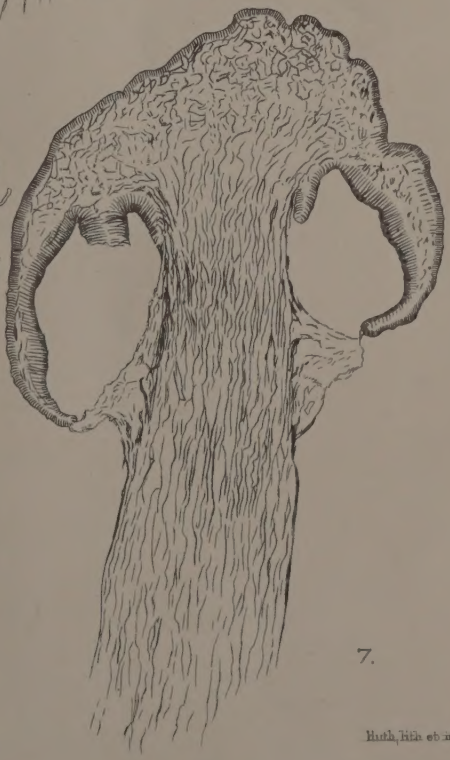

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